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CONTRIBUTIONS ON THE MORPHOLOGY OF THE ACTINOZOA.

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VI. *HALCURIAS PILATUS* AND *ENDOCOELACTIS*.

IN 1892 Carlgren showed that certain Edwardsiae, whose tentacles were more numerous than the mesenteries, had these tentacles arranged on the hexactinian plan, their arrangement in this presumably primitive group of the Actiniaria seeming to foreshadow what is characteristic of the phylogenetically later group. In other multitentaculate Edwardsiae he found what seemed to be an octamerous arrangement combined to a certain extent with hexamerism, but later studies ('99) convinced him that the octamerism did not occur, and that in all cases the hexamerous arrangement obtained.

In the mean time an important discovery had been made by Faurot ('95) in studying *Edwardsia beautempsi* and *E. adenensis*, the former of which possesses fourteen to sixteen tentacles, while for the latter the number is stated to be fifteen to sixteen. Sections through the column showed the eight mesenteries, which have long been supposed to be the only mesenteries developed in the Edwardsiae; but in the uppermost portions a number of additional very short and narrow mesenteries were found which in *E. beautempsi* were placed in such a way as to make with the perfect mesenteries an arrangement recalling what occurs in *Gonactinia prolifera*. Thus there were eight pairs of mesenteries present in the upper part of the column, two of which, the directives, were formed of two perfect mesenteries, four of one perfect and one imperfect mesentery, and one of two imperfect mesenteries. In *E. adenensis* the additional short mesenteries were arranged in pairs in each interval between adjacent perfect mesenteries, except in the endocoel of the directives, so that in this form the arrangement differed somewhat from that typical for the hexactinians.

These observations show reason for believing that in the Edwardsiae there is an intimate relation between the number of tentacles and that of the mesenteries, and that when there are more than eight tentacles there is a strong probability that a number of short mesenteries are also present in the upper part of the column. It is a general rule in the Actininae that the number of tentacles in the fully developed condition is double that of the pairs of mesenteries or, in other words, that there is a tentacle corresponding to each endocoel and each exocoel, the number of tentacles being equal to the total number of mesenteries. Exceptions, due to a lack of development of the full complement of tentacles, are of common occurrence, in many cases probably owing to the specimens examined not having reached their full development, though even in some adults, apparently, the number of tentacles never reaches that of the mesenteries, as is the case, for instance, in *Peachia hastata*, which, with twenty mesenteries, never has more than twelve tentacles.

The rule may be better expressed by saying that *the number of the tentacles never exceeds that of the mesenteries*, and when an apparent exception to this occurs the presumption is that closer examination will reveal the existence of small mesenteries limited to the upper part of the column and in sufficient numbers to fulfill the requirements of the rule.

Acting on this supposition, I have made a further study of the upper portion of the column of *Halcurias pilatus*, a form which I have already described as possessing twenty mesenteries and a number of tentacles considerably in excess of that of the mesenteries, having been estimated in one specimen ('93) to be about seventy, and in another ('98) to be about sixty. Sections showed, as I had expected them to do, the presence of a number of short and narrow mesenteries in the upper part of the column, the number of these *plus* the twenty perfect mesenteries being equal to the total number of the tentacles, which proved to be sixty-eight.

The sections also revealed, however, a peculiarity which I had not expected, and which, as may be seen from Fig. 1, consisted in the short, narrow mesenteries being developed in the

endocoelic spaces bounded by the perfect mesenteries. The sections did not, unfortunately, cut the column perfectly transversely, but the arrangement which obtained may be perceived from the representation of the half of one section shown in Fig. 1, and from the diagram (Fig. 2) which represents a reconstruction from a perfect series of sections. On each side of the median line of Fig. 1 is one of a pair of directives, that to the right being cut at the level of the oral stoma, as is also another mesentery in the right half of the figure. On each side of the



FIG. 1. — Transverse section through the upper part of the column of *Halcurias pilatus*.
T = tentacle. D = directive mesenteries.

directives is a perfect mesentery with its muscle pennon on the same side as that of the adjacent directive, and on the left side this mesentery is succeeded by one which evidently forms with it a typical pair, though it may be noticed that the endocoel enclosed by this pair is broader than the adjacent exocoels. On the right side, where, owing to the obliquity of the sections, the column is cut higher up, the bases of some of the tentacles (T) being cut, the mesenteries of the first lateral pair are widely separated, and between them three imperfect pairs occur, which evidently represent two cycles. The succeeding

exocoel is much narrower than either of the adjacent endocoels and contains no imperfect mesenteries, while in the next endocoel two pairs of mesenteries are seen on the right side and one on the left. By following through the series of sections it is readily seen that the arrangement found in the first lateral endocoel of the right side is repeated in all the others, except in the cases of the endocoels enclosed by the directives, and

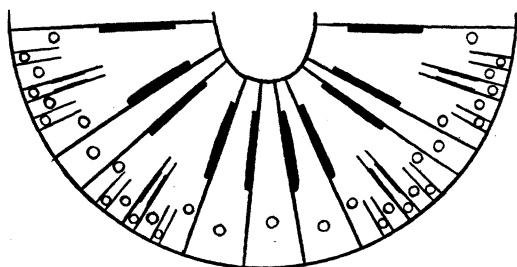


FIG. 2. — Diagram showing the arrangement of the mesenteries and tentacles in *Halcurias pilatus*.

the condition represented diagrammatically in Fig. 2 is that which obtains.

Owing to the relative widths of the endocoels and exocoels, and the presence of imperfect mesenteries in the

former, the first impression one receives is that of a form with a large number of directive mesenteries. That such an interpretation of the conditions is erroneous is clearly shown, however, by reference to the mesenteries on either side of the true directives. It is interesting to note that the development of the imperfect mesenteries, which are plainly arranged in two cycles, follows the hexactinian rule, the smaller pairs being developed in the intervals between the larger pairs and the adjacent perfect mesenteries. It may be added that my sections show the existence of a marginal stoma in each perfect mesentery in addition to the oral stoma already mentioned.

From the description given above, it will be perceived that the arrangement of the mesenteries in *Halcurias pilatus* is identical with that described by Carlgren ('97) for a form from the Chinese seas which he refers to the genus *Endocoelactis* and to a new family, the Endocoelactidae. The similarity to *Halcurias* is by no means confined, however, to the arrangement of the mesenteries, and there can be no question but that the two forms must be referred to the same genus, to which, notwithstanding the greater appropriateness of Carlgren's name, the prior term, *Halcurias*, must be applied. The

specific identity of Carlgren's form with *H. pilatus* seems improbable; for, apart from the difference in the localities for which the two have been obtained, the tentacles of the Chinese form are longer apparently than those of *H. pilatus*, and to judge from Carlgren's figures, the longitudinal musculature of the tentacles is weaker and its mesogloal processes coarser. It seems preferable at present to regard them as distinct, and since Carlgren, in his brief notice, has bestowed no specific name on his *Endocoelactis*, I would suggest that it be named *Halcurias Carlgreni*, as a slight recognition of the admirable work which that author has accomplished on the morphology of the Actiniaria.

An examination of the arrangement of the tentacles of *H. pilatus* with reference to the mesenteries was made in the series of transverse sections and also by an examination of the disk, and the results obtained were essentially the same as Carlgren's. I was not able, however, to distinguish any difference in the position of the tentacles over the endocoels bounded by the imperfect mesenteries, though on theoretical grounds it is probable that some difference does exist, and, furthermore, the study of sections seemed to indicate that the tentacles over the directive endocoels were situated a little nearer the mouth than were the others represented as being in the same cycle in Fig. 2; an examination of the disk failed, however, to confirm this appearance.

As regards the systematic position of *Halcurias*, a few remarks are in order. I at first ('93) assigned it to the family Halcampidae, but later ('98) deemed it advisable to separate it from that family and refer it to Hertwig's Antheomorphidae. Carlgren in the mean time had established for his *Endocoelactis* the family Endocoelactidae. There are apparently three courses open for the disposal of the genus. It may be referred to a family already existent, the definition of the family being changed, if necessary, to accommodate it; or it may be taken as the type of a distinct family, as Carlgren has done; or, finally, it may be separated altogether from the Hexactiniae and regarded as the type of a separate tribe.

It seems to me that this last procedure is quite unnecessary,

and would probably be entirely out of harmony with the phylogenetic relationships of the genus. We have learned within recent years how extensively nearly allied forms may differ, and how great are the modifications which the hexactinian type may undergo. The entire facies of *Halcurias* is that of an hexactinian, and it may furthermore be pointed out that instances of the occasional endocoelous development of mesenteries have been already recorded by G. Y. and A. F. Dixon ('89) in *Bunodes thallia* and by Haddon ('98) in *Actinioides dixoniana* and *A. papuensis*.

If, then, the third possibility be excluded, *Halcurias* must either be assigned to an existent family, the endocoelous development of mesenteries being regarded as of minor importance, or this feature may be considered of sufficient importance to warrant the establishment of a separate family. I have already indicated my belief that the peculiar mode of development of the secondary and tertiary mesenteries is of minor importance and see no more reason for separating *Halcurias* as the type of a new family than I do for separating an octamerous sagartian, or one with a multiplicity of mouths and many siphonoglyphs, from the rest of the members of that family.

It remains then to consider what the forms may be with which *Halcurias* may be associated. As Carlgren has remarked, and as I have indicated by the position to which I have referred it in previous papers, *Halcurias* occupies a position near the base of the hexactinian stem. The small number of perfect mesenteries, the occurrence of reproductive organs on all of them, the absence of a distinct sphincter muscle, the simplicity of the margin, are features which, when combined in one individual, indicate for it a somewhat low position. Are there other forms which present a similar combination of peculiarities associated with the development of an adherent base?

Two forms suggest themselves in this connection, namely, *Gonactinia prolifera* and *Protanthea simplex*; but both of these present peculiarities which render their association with *Halcurias* inadvisable. They both have but eight perfect mesenteries, the remaining ones, eight in *Gonactinia* and about

eighty-eight in *Protanthea*,¹ being imperfect, and the ciliated lobes are lacking in their mesenterial filaments. On account of these peculiarities it seems to me that these two forms must be grouped together in a family, Gonactiniidae, as Carlgren ('93) has proposed, and *Halcurias* cannot be placed with them. The family Gonactiniidae must, I believe, be placed among the Hexactiniae, as indeed must all the forms which I have included in the past in the order Protactiniae, as well as those which Carlgren has referred to the Protantheae. The discovery of hexactinian mesenteries in certain Edwardsiae, already referred to, necessitates either the abolition of both this order and that of the Protactiniae, or else an extension of the latter to include both the Edwardsiae and many of the Halcampidae, and it seems to me that the former step is the most practical and the most in accord with a correct phylogenetic scheme. Not that I mean by this that the stages of development shown by the members of the group do not represent phylogenetic stages in the evolution of the Hexactiniae. Certainly no one will imagine that what has so long been regarded as the Edwardsian type of structure is not in reality a primary phylogenetic condition, even though we are now obliged to regard the existing Edwardsiae as true hexactinians which secondarily in some cases may represent the more primitive condition.² The facts of embryology speak too strongly regarding the Edwardsian stage to allow of question as to its past occurrence, and I believe that there can be as little question regarding the stages which I have supposed to intervene between the Edwardsiae and the typical Hexactiniae, even though the forms which to-day represent these stages do so possibly only on account of secondary modifications.

¹ *Protanthea* has four imperfect mesenteries which make pairs with the four lateral perfect mesenteries, and twelve others arranged in pairs in the primary exocoels, all being fertile and provided with mesenterial filaments. In addition to these there are, however, as in *Halcurias*, a number of short, narrow mesenteries confined to the upper part of the column and standing in relation to the tentacles, of which there are about ninety-six.

² Compare Van Beneden, Les Anthozoaires in Ergebnisse der in dem Atlantischen Ocean, etc., ausgeführten Plankton-Expedition der Humboldt-Stiftung. II. 1898.

It seems inadvisable then to associate *Halcurias* with *Gonactinia* and *Protanthea*, but there still remains a possible association with Hertwig's Antheomorphidae. Unfortunately the forms upon which this family was founded are insufficiently known, but it seems to me that there are reasons for maintaining the position I have already ('98) advocated, that the nearest allies of *Halcurias* at present known are to be found in the family Antheomorphidae. I find myself obliged, however, to recede from the position I held in 1898 as to the distinctness of this family and to return to my earlier opinion, which has received the approval of so critical a taxonomist as Haddon ('98), that the Antheomorphidae should be included in the family Actiniidae, and if this view be accepted it is necessary to refer the genus *Halcurias* to that family also.

This will necessitate no important modification of the definition of the Actiniidae given by Haddon ('98), but as I shall have occasion in the immediate future to consider the family in some detail, I shall postpone a discussion of its delimitation for the present.

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November 10, 1900.

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